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Historical Zoogeography and Taxonomic Status of the Prairie Vole (*Microtus ochrogaster*) from the Southern Plains of Texas and Oklahoma

Frederick B. Stangl, Jr., Jim R. Goetze, and Kimberly D. Spradling

The prairie vole (*Microtus ochrogaster*) today is considered a species of the Great Plains, whose range extends from the interior grasslands of southern Canada to central Oklahoma and the northern Texas Panhandle, and is generally bordered by the Rocky Mountains to the west and the eastern deciduous woodlands (Bee et al. 1981; Hall 1981; Hoffmann and Koeppl 1985; Caire et al. 1990; Stalling 1990). During the late Pleistocene, the species occurred throughout much of Texas, leaving fossil evidence as far south as the Edwards Plateau and parts of the Gulf Coast (Dalquest and Schultz 1992; Graham 1987). The species retreated northward with the advent of increasingly arid climate during the Holocene. At least one isolated population, *M. o. ludovicianus*, was stranded during this time, and is known to have survived in extreme southeastern Texas and adjacent Louisiana until the earliest 1900s (Bailey 1905).

Hibbard and Rinker (1943) reported a series of *M. ochrogaster* taken in 1942, which extended the known range of the prairie vole southward into Meade County of southwestern Kansas. The animals were found to be restricted to the few bogs and meadows, having survived increasing pressures of agriculture and a recent drought. On the basis of these specimens, considered by them to represent a relictual population with distinct cranial characters and pale pelage coloration, they described *M. o. taylori*.

Choate and Williams (1978) performed a morphometric analysis of the prairie vole, which included material reported on by Hibbard and Rinker (1943) as *M. o. taylori*. Each of their external body measurements and four of the seven cranial characters (skull length, zygomatic breadth, mastoidal breadth, and least interorbital breadth) exhibited significant geographic variation. While no geographic patterns were evident to suggest subspecific levels of differentiation, populations from the Dakotas to Kansas demonstrated a slight north-to-south clinal increase in size of cranial characters. Among their conclusions were that the population referred to as *M. o. taylori* by Hibbard and Rinker (1943) no longer exists. They hypothesized that either the type locality and vicinity was colonized by adjacent populations following extirpation of the original *taylori* stock by drought, or that genetic swamping enveloped the few remaining drought survivors. Consequently, in their view, all *M. ochrogaster* from the Central Plains (which would include all prairie voles of Nebraska, Kansas, Colorado, and Oklahoma) should be assigned to the subspecies *M. o. haydenii*.

Since 1986, populations of the prairie vole have been reported from south-central Oklahoma (Choate 1989; Smith 1992a), and the panhandles of Oklahoma (Dalquest et al. 1990a; Reed and Choate 1988) and Texas (Choate and Killebrew 1991; Jones et al. 1988; Manning and Jones 1988). Each of these populations represents marginal extensions to the south of the previously mapped ranges of the species. Reed and Choate (1988) suggested that their Oklahoma panhandle specimens represented an invasion by *M. o. haydenii* stock, but others (Dalquest et al. 1990a; Manning and Jones 1998) have tentatively referred specimens from the Oklahoma and Texas panhandle regions to *M. o. taylori*.

Presence of the prairie vole in southern Oklahoma first was documented by Choate (1989), who considered the south-central Oklahoma prairie vole population from the Wichita Mountains to be a relict of the late Pleistocene or early Holocene. He referred his specimens to *M. o. haydeni* on geographic grounds. Even at a glance, the pelage coloration of these animals is dark--comparable to reference series from Kansas, Nebraska, and Missouri--and in striking contrast to the pale pelage of specimens from southern Colorado and the panhandle regions of Oklahoma and Texas.

This study characterizes the morphometric variation of southern peripheral populations of prairie voles, and provides the first critical review of the species to include specimens from Texas and Oklahoma. We examine the historical zoogeography and subspecific status of the species from those states, with special attention to the question of *M. o. taylori* as an extant taxon and its validity as a subspecies.

MATERIALS AND METHODS

Specimens of *Microtus ochrogaster* from the collections of Midwestern State University, Texas Tech University, and Oklahoma State University were surveyed from southern localities of the species' range. Of these, 129 specimens representing adult individuals (two oldest of four age classes, *sensu* Choate and Williams 1978) taken from three populations at the southern periphery of the species' range in Oklahoma and Texas (Figure 1), and reference series from Colorado (western peripheral population) and Kansas (interior sample) were selected for final study. Each of the three nominal subspecies (*sensu* Hall 1981; Hoffmann and Koeppl 1985; Stalling 1990) are represented in the analyses: *M. o. taylori* from the Texas and Oklahoma panhandles; *M. o. haydenii* from southern Colorado and southern Oklahoma; and *M. o. ochrogaster* from eastern Kansas. However, we note that Choate and Williams (1978) have synonymized *M. o. ochrogaster* with *M. o. haydenii*, and we follow their revision.

Seven cranial measurements described by Choate and Williams (1978; length of skull, zygomatic breadth, mastoidal breadth, least interorbital breadth, prelambdoidal breadth, length of rostrum, and maxillary toothrow) were taken with digital calipers and recorded to the nearest 0.01 mm. We depart from their protocol by excluding standard body measurements on the basis of inescapable variations in methodology and skills of different preparators.

Sexes were pooled for all subsequent analyses after two-way (sex, age) multiple analysis of variance (MANOVAs) for each measurement revealed that sexual dimorphism and interactions between age and sex were not significant.

Age variation between the two adult age classes in our study was significant for each character except least interorbital breadth and prelambdoidal breadth (one-way MANOVAs; $P = 0.2987$ and $P = 0.1779$, respectively), and only the least interorbital breadth (one-way MANOVA, $P \leq 0.0001$) among young adult specimens exhibited significant geographic variation. Based on these findings, further geographic analyses were restricted to four samples comprised of specimens representing the oldest of the four age categories. Only for the Oklahoma/Texas panhandles sample was it necessary to pool individuals from more than one collecting locality.

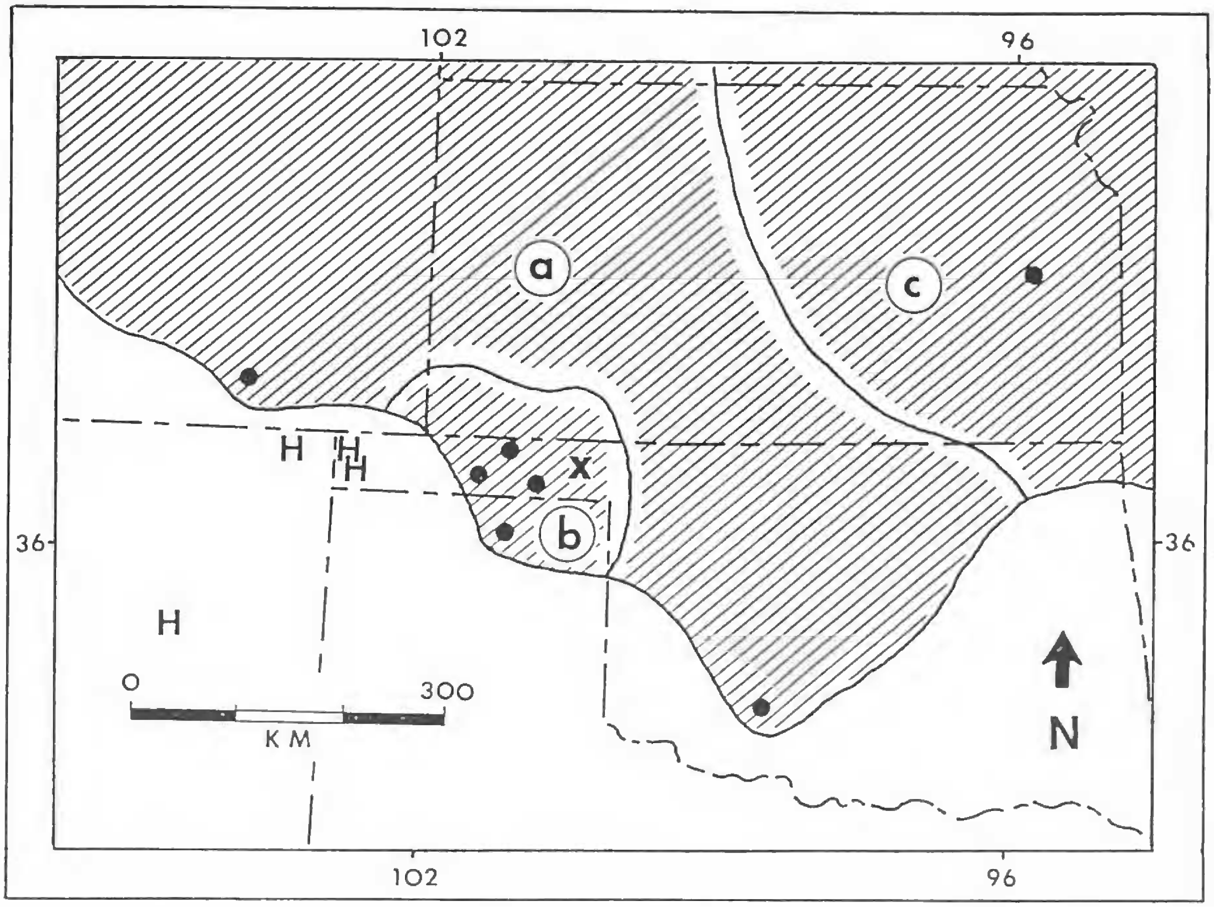

Figure 1. Southern distribution and superimposed locality records for *Microtus ochrogaster*. Holocene records from Dalquest et al. (1990b) are indicated by "H". Site represented by skulls examined from owl pellets is indicated by "X". Nominal subspecific taxa (*sensu* Hall 1981) represented are: a) *M. o. haydenii*; b) *M. o. taylori*; and c) *M. o. ochrogaster*.

Principal components analysis of the covariance matrix was used to assess patterns of geographic variation between populations, and discriminant functions analyses were applied to assess uniformity of distinctness of those samples. Duncan's Multiple Range tests were used to examine morphometric associations between populations. All computations were accomplished with NCSS, Version 5.3 (Hintze 1990).

Specimens examined.--Following is the list of "old adult" individuals (*sensu* Choate and Williams, 1978), listed by nominal subspecific designation, that comprise the basis for this study: *M. o. haydenii*--COLORADO: Huerfano Co., 4 mi. W Walsenburg, 6 (MWSU 18156-18159, 18161, 18162); OKLAHOMA: Comanche Co., Fort Sill, Wichita Mountains, 30 (MWSU 14219, 14221, 14222, 14224, 14226, 14431, 14463, 14474, 14476, 14569, 14632, 14633, 14741, 14776, 14777, 14854-14856, 14858-14860, 14862, 14872, 14873, 15018, 15019, 15068, 15069, 15594, 15741); *M. o. ochrogaster*--KANSAS: Franklin Co., 1-5 mi. S Ottawa, 19 (MWSU 5367, 5368, 7176-7180, 7191, 7483-7485, 9186, 9188, 9192-9197, 15960); *M. o. taylori*--OKLAHOMA: Beaver, Co., 3.8 mi. W Bryan's Corner, 1 (MWSU 16508); Texas Co., 11.1 mi. E Guymon, 1 (MWSU 15674); 4 mi. NE Tyrone, 2 (MWSU 15715, 15735); TEXAS: Hansford Co.: 8 mi. S Spearman, 4 (TTU 52211, 52449, 52450, 52423). Specimens from Texas are deposited in The Museum of Texas Tech University (TTU), and all others are from the Collection of Recent Mammals at Midwestern State University (MWSU).

RESULTS

Each of the cranial characters, except zygomatic breadth in old adult *Microtus ochrogaster*, exhibited highly significant geographic variation between the studied populations (Table 1). The interior sample from Kansas averaged smaller than any peripheral population for five of the seven measured characters. These differences are significant (Duncan's Test at $P \leq 0.05$ level) for length of skull, rostral length, and length of maxillary toothrow. Colorado is represented by an assemblage of particularly robust specimens, averaging

*Table 1. Comparison of cranial measurements (in mm) of 63 "old adult" specimens of the prairie vole (*Microtus ochrogaster*) from four southern populations. Descriptive statistics are sample size (N), arithmetic mean, standard deviation (SD), extreme measurements (minimum-maximum), confidence intervals (CI), and coefficients of variation (CV).*

Character	Texas/Oklahoma panhandles (N = 8) Mean±SD (Min. -max.) 95% CI CV	Wichita Mountains, southern Oklahoma (N = 30) Mean±SD (Min. -max.) 95% CI CV	Huerfano Co., southern Colorado (N = 6) Mean±SD (Min. -max.) 95% CI CV	Franklin Co., eastern Kansas (N = 19) Mean±SD (Min. -max.) 95% CI CV
Skull length **	28.60±0.94 (27.29-30.13) 27.82-29.39 3.29	28.38±0.70 (26.52-29.64) 28.12-28.65 2.47	28.52±0.83 (28.77-30.80) 28.52-30.25 2.82	27.33±0.76 (25.71-28.56) 27.00-27.67 2.56
Zygomatic breadth N.S.	16.09±0.74 (15.18-17.15) 15.48-16.70 4.58	15.99±0.51 (14.92-17.03) 15.79-16.18 3.16	16.12±0.28 (15.80-16.53) 15.83-16.41 1.72	15.59±0.43 (14.70-16.32) 15.38-15.79 2.75
Mastoid breadth **	12.27±0.45 (11.84-13.87) 11.89-12.64 3.70	12.63±0.31 (12.05-13.27) 12.51-12.75 2.47	12.36±0.23 (12.14-12.74) 12.11-12.60 1.88	12.16±0.35 (11.58-12.74) 11.99-12.33 2.90
Interorbital breadth **	3.86±0.31 (3.16-4.15) 3.61-4.12 3.70	4.31±0.19 (3.90-4.71) 12.51-12.75 2.47	4.16±0.16 (4.06-4.47) 12.11-12.60 1.88	4.17±0.22 (3.69-4.69) 11.99-12.33 2.90
Prelamdoidal breadth **	9.89±0.46 (9.13-10.50) 9.50-10.27 4.69	10.52±0.27 (7.65-9.36) 10.42-10.63 2.54	10.33±0.38 (8.93-9.84) 9.94-10.73 3.66	10.14±0.41 (7.42-8.62) 9.94-10.33 4.00
Rostral length **	8.77±0.35 (8.23-9.19) 8.48-9.06 3.94	8.62±0.38 (7.65-9.36) 8.48-8.76 4.34	9.24±0.39 (8.93-9.84) 8.82-9.65 4.25	8.00±0.36 (7.42-8.62) 7.83-8.18 4.52
Maxillary toothrow length **	6.41±0.31 (6.02-7.01) 6.15-6.66 4.81	6.42±0.22 (6.07-6.94) 6.34-6.51 3.45	6.68±0.07 6.56-6.79) 6.60-6.76 1.13	6.16±0.27 (5.52-6.70) 6.02-6.29 4.38

One-way MANOVA: ** = $P \leq 0.001$

significantly larger than all other populations for zygomatic breadth, rostral length, and maxillary toothrow. The southern Oklahoma population is significantly largest for mastoid, interorbital, and prelambdoidal measurements. The pooled sample from the Texas and Oklahoma panhandles is most variable with highest coefficients of variation for all measurements but rostral length, and is characterized by a significantly narrow least interorbital breadth.

The first three principal components accounted for 81.6% of the total variation between populations. Of the two-dimensional scatterplots examined, the first two components provided clearest separation of specimens by region-of-origin (Figure 2). All characters but prelambdoidal and interorbital measurements were highly correlated with the first factor, which contributed more than half (51.1%) of the reported variability. The second factor accounted for 19.9% of the variation, and was most influenced by prelambdoidal, mastoidal, interorbital, and zygomatic measurements. The third factor accounted for 10.6% of the variation.

Discriminant functions analysis of the seven cranial measurements from all four samples served to accurately predict the geographic origin for 81% (50 of 62) of the individuals. When this analysis was restricted to the three peripheral populations (exclusion of the Kansas sample), 88% were correctly assigned to locality. Misclassifications occurred within each sample and appeared to be random in effect.

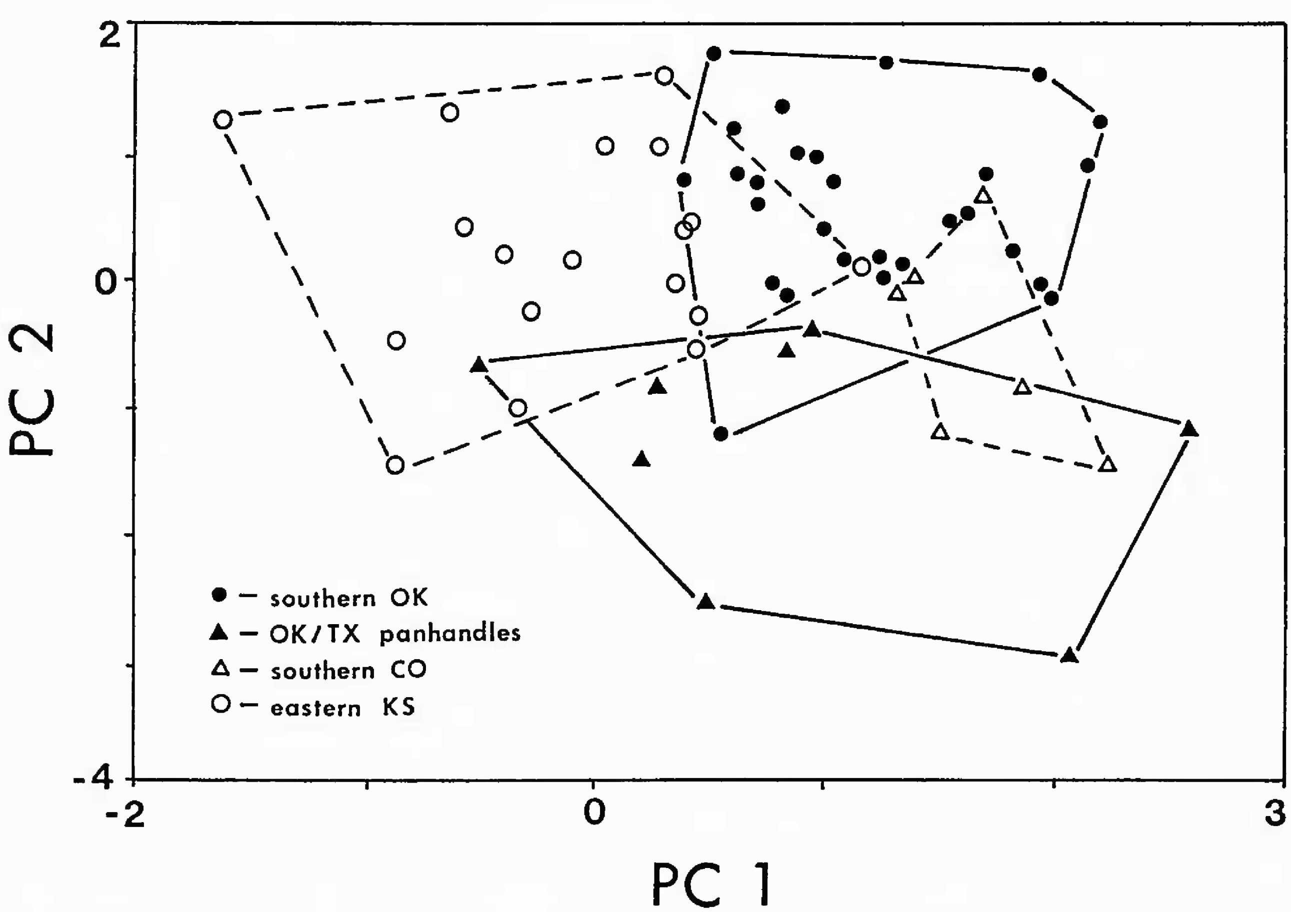

Figure 2. Scatter plot of first two principal components for four populations of *Microtus ochrogaster*.

DISCUSSION

Historical Climatology

The southern Great Plains of the late Pleistocene was a cooler, moister, and more equable time than the prevailing conditions of today (Graham 1987). Pollen records suggest that expanses of sandsage (*Artemisia*) grasslands dominated the western High Plains, and comparatively mesic prairies cloaked the Rolling Plains of Texas and Oklahoma to the east. These vegetation associations likely had no modern analog (Hall and Valastro 1995), but conditions clearly favored such mesic grasslands forms as *Microtus ochrogaster*; its remains occur in Pleistocene sediments throughout the region.

Emergence from the Pleistocene into a warmer and drier Holocene has been anything but gradual and regionally uniform. Studies of sedimentary deposition and erosion across numerous sites of the High Plains of the Texas Panhandle suggest a prolonged drought between 6,500 and 4,500 YBP (Holliday 1989). Evidence from buried trees and water table fluctuations in the canyons of the southern Oklahoma Rolling Plains (Hall and Lintz 1984) indicate a local shift to a moister environment about 2,600 YBP, which coincides with a mesic interlude in the desertification of Trans-Pecos Texas (Bryant 1977). These conditions apparently lasted until about 1,000 YBP, which marked the advent of the modern trend toward increasing semiarid conditions (Hall and Lintz 1984).

Historical deviations from the current progression towards a progressively warmer and drier environment are sometimes of considerable duration and magnitude. The "Little Ice Age" of 1450-1890 A.D. was a period of increased precipitation and cooler temperatures that was apparently global in effect (Crowley and North 1991).

Modern weather patterns of the Southern Plains are subject to dramatic fluctuations, and can vary regionally. Sustained temperature extremes over weeks or months, and droughts of up to several years in duration, are not uncommon, and each can have a locally devastating effect on resident species. However, few significant long-term changes in annual mean climatic variables have occurred over the Southern Plains during the past century (Figure 3), with the exceptions of warming in Lubbock, cooling in Wichita Falls, and increasing moisture in Oklahoma City.

Historical zoogeography of southern peripheral populations

Southern Oklahoma.—The southernmost population of *Microtus ochrogaster* may well have occupied the Wichita Mountains of south-central Oklahoma continuously since the Pleistocene. The fossil record in the immediate vicinity is problematic, for the loose teeth that usually represent this species in fossiliferous strata cannot be distinguished from those of the woodland vole (*M. pinetorum*), a locally sympatric species that also occurs in the Pleistocene. Holocene deposits from two locations within 30 miles of these hills, and dated at 2,000 YBP, contain microtine remains that might be either of these species (Goetze 1989; Smith 1992b). However, each of these two sites also contained the remains of prairie indicator species (thirteen-lined ground squirrel, *Spermophilus tridecemlineatus;* hispid pocket mouse, *Chaetodipus hispidus;* hispid cotton rat, *Sigmodon hispidus*), suggesting that at least some of these microtine teeth might represent *M. ochrogaster*.

The rugged granite hills, a mesic refugium marked by wooded slopes and rocky soils, were never as attractive as the surrounding level plains to homesteaders of the 1880s, thereby protecting comparatively lush grassy parks from the plow and extensive overgrazing.

The prairie vole only rarely is encountered elsewhere today in southern Oklahoma beyond the Wichita Mountains (Smith 1992a; Stangl et al. 1992), but it is locally common within the protective confines of these hills, from where it was first reported by Choate (1989). Absence of any earlier documentation seems only a matter of the lack of systematic collecting, as is evident from an earlier compilation of small mammal records from the Wichita Mountains by Glass and Halloran (1961). Much of this isolated range of this vole falls within the boundaries of the Wichita Mountains National Wildlife Refuge (first established as a national forest in 1901) and Fort Sill (an army installa-

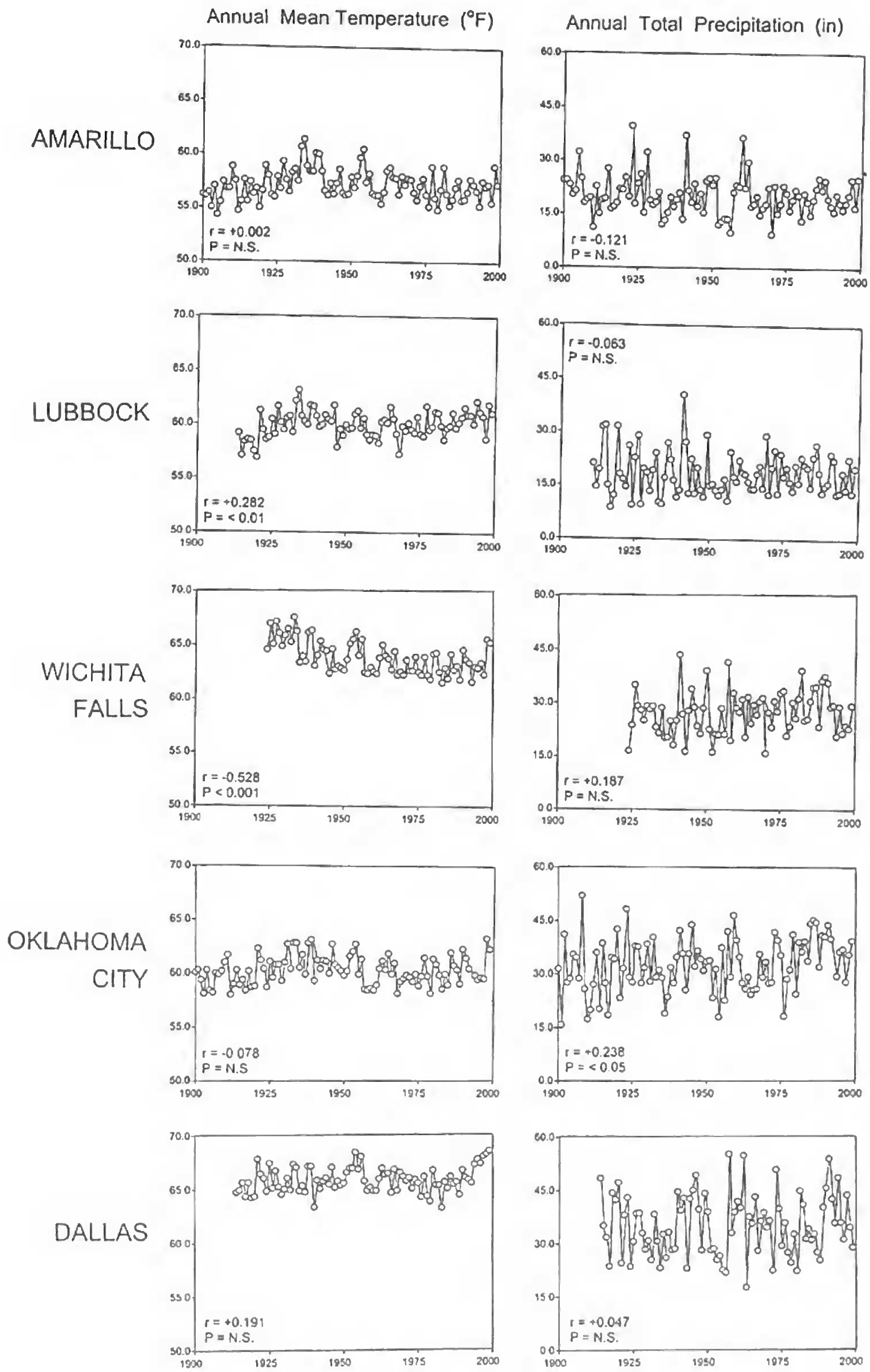

Figure 3. One-hundred year weather trends from five cities in Texas and Oklahoma that bracket the southern periphery of the range of *Microtus ochrogaster*. Data of annual means for temperature and precipitation are from National Atmospheric and Oceanic Administration.

tion of 98,000 acres, established in 1869), which today provide security for this relict population.

Texas/Oklahoma panhandles.—The semiarid short-grass prairies of the High Plains provide marginal habitat today for the prairie vole. The fact that recent range extension reports in the region (Manning and Jones 1988; Reed and Choate 1988; Dalquest et al. 1990a; Choate and Killebrew 1991) are from along transportation routes may be significant. Fencerows, pavement runoff, and water collection along railroad and highway rights-of-way promote comparatively lush vegetation. These conditions offer both adequate conditions and avenues of dispersal, as well as protection from livestock overgrazing on adjacent rangelands that are, in any event, privately owned and not usually accessible to collectors.

The semiarid short-grass prairie of the High Plains currently occupied by western peripheral populations of the prairie vole provide only locally marginal habitat. The history of the prairie vole in the Texas/Oklahoma panhandles and adjoining parts of Colorado, New Mexico, and Kansas extends well back into the Pleistocene (Hibbard 1949; Graham 1987; Dalquest and Stangl 1989; Dalquest and Schultz 1992). Several extralimital carbon-dated Holocene deposits (Dalquest et al. 1990b) from the Oklahoma Panhandle and northeastern New Mexico (Figure 1) document the presence of *M. ochrogaster* at various times during an interval of at least 3,860-530 YBP. This does not necessarily suggest a continuous regional occurrence of the prairie vole, but more likely, a period of time during which the species locally has experienced a long ebb-and-flow history of peripheral range fluctuations.

One-hundred year weather data for the region (Figure 3) demonstrate few significant weather trends over that period, although pronounced episodes such as the Dust Bowl era and droughts of the late 1990s have occurred in the interim. The discovery of *M. ochrogaster* by Hibbard and Rinker (1943) in southwestern Kansas came after the 1930's Dust Bowl era, and extended the known range into extreme southern Kansas at a time when local populations were apparently restricted to lush growth fringing the few remaining isolated bogs of the region.

It is difficult to discern if the more recent discoveries since the late 1980s to the south, in the Texas/Oklahoma panhandles, represent a reclamation of earlier abandoned range, or simply the discovery of the species in an area that has only in the past two decades been systematically collected. Earlier and more occasional collecting efforts might have easily overlooked this locally uncommon and sporadically distributed species.

Taxonomic status of Southern Plains prairie voles

The morphometrically distinct nature of each of the four populations examined is consistent with the findings of Choate and Williams (1978) from across the northern range of *Microtus ochrogaster*, and represents a continuum of the patterns of distribution observed by those authors. We attribute the magnitude of differentiation of specimens in our study area to the degree of isolation expected from a less-than-uniform distribution at the periphery, where conditions are generally marginal at best. Areas of occupation are probably best portrayed as scattered isolates or tendril-like extensions into areas of suitable habitat--with little or no lateral gene flow. With the exception of Texas/Oklahoma panhandle populations, we follow Choate and Williams (1978) in referring prairie voles from this study to *M. o. haydenii,* because these populations seem only to represent the extreme of a cline of morphometric differentiation and increase in size. However, the distinctive population referred to as *M. o. taylori* by Hibbard and Rinker (1943) remains an extant entity.

In their original diagnosis of *M. o. taylori*, Hibbard and Rinker (1943) placed considerable emphasis on the distinctive interorbital ridge. Choate and Williams (1978) correctly noted that the development of this feature is a function of the distinctively narrow interorbital breadth (IOB) of *M. o. taylori*. This is clearly evident with the illustrations provided by Hibbard and Rinker (1943:257, Figure 1), and yet they failed to refer specifically to the comparatively narrow IOB, or to include that character in their diagnosis.

The extreme constriction of the interorbital breadth is a defining and readily visible feature of *M. o. taylori*, and one which exemplifies specimens taken in recent years from the Texas/Oklahoma panhandles (Table 1). Fortunately, this component of the skull is durable, and often remains intact after disintegration and loss of other cranial components (Stangl et al. 1993), and is a character that does not usually differ by age or sex in the prairie vole (Choate and Williams 1978). This permits us to assign the fragmented remains from owl pellets (N = 10, mean = 3.94) reported by Dalquest and Baskin (1991) from the Oklahoma Panhandle to *M. o. taylori*. Similarly, we can date this subspecies back to at least 530 $\pm$ 60 YBP from Trampiros Creek of Union Co., New Mexico (Dalquest et al. 1990b), on the basis of the fortuitous preservation and recovery of the braincase of a specimen (IOB = 3.82) from ancient pond sediments.

Of particular interest is the status of southwestern Kansas populations. The utility of the IOB measurement as a diagnostic tool transcends both spatial and temporal bounds, does not vary by sex or age in the prairie vole (Choate and Williams 1978) and can be applied to all but the most damaged and fragmentary skull. It should prove useful to test the hypothesis of Choate and Williams (1978)--that *M. o. haydenii* is the current prairie vole of southwestern Kansas, having occupied the historical range of *M. o. taylori.*

Peripheral populations and large size in microtine rodents

Finally, we note that the especially large and robust nature of peripheral *Microtus ochrogaster* populations is not unusual among voles. This phenomenon has been demonstrated in peripheral populations for an array of microtine taxa, suggesting that increased size confers some locally adaptive advantage for coping with the stresses of existing in marginal habitat that could logically pertain to the periphery of a species' range.

In support of his proposed model of centrifugal speciation, Brown (1957) noted that peripheral populations of European microtines tended to be more variable and larger in size than their interior counterparts. Chitty (1958) initiated a series of studies (later summarized by Krebs [1978]) which detailed the attainment of large size of a suite of morphological characters among microtine populations as an adaptive response to environmental stress. More recently, exceptionally large size was noted for individuals among populations of *M. californicus* recovering from the rigors of peak densities, and usually associated with poor habitat (Lidicker and Ostfeld 1991).

The large size of Southern Plains prairie voles is certainly consistent with the clinal increase in size reported by Choate and Williams (1978) for the species, but are the stresses of "life on the frontier" contributory? Examination of peripheral populations of this species to the north, east, and west could prove informative.

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Addresses of authors:

FREDERICK B. STANGL, JR.

Department of Biology
Midwestern State University
Wichita Falls, Texas 76308
email: frederick.stangl@mwsu.edu

JIM R. GOETZE

Science Department
Laredo Community College
Laredo, Texas 78040
email: jrgzoo@lmtonline.com

KIMBERLY D. SPRADLING

Department of Biological Sciences
University of North Texas
Denton, Texas 76203
Email: kds0052@unt.edu